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PERSPECTIVE

THE SUCCESS OF FAILED *HOMO SAPIENS* DISPERSALS
OUT OF AFRICA AND INTO ASIA

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Ryan J. Rabett

The evidence for an early dispersal of *Homo sapiens* from Africa into the Levant during Marine Isotope Stage 5 (MIS-5) 126-74 ka (thousand years age) was characterised for many years as an 'abortive' expansion: a pre-cursor to a sustained dispersal from which all extant human populations can be traced. Recent archaeological and genetic data from both western and eastern parts of Eurasia and from Australia are starting to challenge that interpretation. This short paper reviews current evidence for a scenario where the MIS-5 dispersal encompassed a much greater geographic distribution and temporal duration. The implications of this for tracking and understanding early human dispersal in Southeast Asia specifically are considered, and the validity of measuring dispersal success only through genetic continuity into the present is examined.

The recovery of early *Homo sapiens* fossils from sites in the Wadi-el-Mughara of northern Israel, initiated by Garrod in the late 1920's, and at Qafzeh cave in lower Galilee by Neuville (1932-1935) and Vandermeersch (1965-1979), provided rich grounds for investigating historical questions about the role of the Levant in late human evolution and its use as a corridor for Upper Palaeolithic dispersal into western Europe^{1,2}. A suite of radiometric dates obtained at these sites over the last 25 years, however, has consistently placed their occupation within MIS-5³⁻⁸. The recent discovery of a human calvarium that has been

provisionally dated to 54.7 ± 5.5 ka (all dates in this paper are in calendrical years unless otherwise stated) from Manot Cave, Israel, an which bears morphological affinity to European Upper Palaeolithic populations may be a sign that the full picture of this geographic relationship has yet to emerge⁹. The Skhūl and Qafzeh fossils remain, however, chronologically remote from the earliest appearance of *H. sapiens* in Eurasia, currently thought to be *c.* 47 ka or slightly earlier¹⁰. Uranium-series (U-Series) and Electron Spin Resonance (ESR) direct-dating of the Skhūl II and V skeletons suggests that burial took place $98^{+19/-10}$ ka⁴. At Qafzeh, the fossil-bearing stratigraphy (Layers XVI-XXI) has returned U-Series dates of 103 ± 19 ka and 105 ± 02 ka⁵, and Thermoluminescence (TL) dates on burnt flints (Layers XVII-XXIII) of between 82.4 ± 7.7 ka and 109.9 ± 9.9 ka⁸.

A clear separation between an initial and then later sustained dispersals of early *H. sapiens* into Eurasia also features prominently in our expanding genetic coverage of early humanity. On these grounds there continues to be confidence in the assertion that MIS-5 migrants did not contribute to the extant human genepool¹¹⁻¹³. Both the genetic and the archaeological evidence have tended to support an interpretation that the Levantine palaeo-deme represented a precociously early, geographically local and ultimately ill-fated dispersal from Africa¹⁴⁻¹⁶. Worsening climate is often cited as an explanatory driver that prompted either range contraction back into the African continent, or else extirpation of this population^{16,17}. As the early story of our species continues to be uncovered, humanity's initial emergence and spread even within this one continent, though, is becoming increasingly complex, ancient and pan-African in perspective¹⁸⁻²⁰; potential indications that whatever the narrative of our wider dispersal, we should expect it to be similarly multifarious.

It was speculated some time ago that the early *H. sapiens* record from the Levant could have been part of a wider migration⁷. Under that scenario, the disappearance of groups from the Levant need not necessarily have signalled range contraction or extra-African extinction. The extent and longevity of such a dispersal, particularly if it was ultimately un-sustained, would raise important questions about the assumed link between anatomically modern human behavioural capacity and our global diaspora; and more fundamentally, about how we should measure evolutionary success. Data now accumulating from across Eurasia, and particularly from Southeast Asia (Sunda) and Greater Australia (Sahul) (Fig. 1, Table 1), make it feasible to entertain such a possibility more seriously and to consider its implications.

Fig. 1, map showing the location of sites discussed in the text. See Table 1 for the list of locations and a breakdown of the associated evidence as illustrated on the map.

Table 1, Archaeological, fossil and genetic evidence from sites discussed in the text and presented in Fig. 1. (Note that the type of finds listed does not necessarily constitute the sum of evidence recovered from any given site.)

Site number	Site name	Type of find
1	Wadi-el-Mughara + Qafzeh	Hominin fossils
2	Manot Cave	Hominin fossil
3	MDF-61	Stone tools (Middle Palaeolithic – MP)
4	Jebel Qattar 1	Stone tools (MP)
5	Kachchh Peninsula	Stone tools (MP)
6	Katoati	Stone tools (MP)
7	Jwalapuram 3	Stone tools (MP)
8	Callao Cave	Hominin fossil

9	Tam Pa Ling	Hominin fossils
10	Lida Ajer	Hominin fossil
11	Madjedbebe	Edge ground stone tools, plant processing
12	Tabon Cave	Hominin fossils
13	Niah Caves	Hominin fossils, plant processing
14	Warraty rock shelter	Stone tools
15	Riwi Cave	Marine fauna (shell)
16	Hang Thung Binh 1	Marine fauna (shell –river mouth)
17	Phia Vai Cave	Marine fauna (shell)
18	Golo Cave	Marine fauna (shell)
19	Leang Timpuseng	Rock art
20	Jerimalai rock shelter	Marin fauna
21	Matja Kuru 2	Hafted bone point
22	Fuyan Cave	Hominin fossils
23	Punung III	Hominin fossil
24	Denisova Cave	Hominin DNA
25	Vindija Cave	Hominin DNA
26	Mal'ta	Hominin DNA
27	Ust'-Ishim	Hominin DNA
28	Kostenki	Hominin DNA
29	Tianyuan Cave	Hominin DNA
30	Darra-i-Kur	Hominin DNA
31	Chertovy Vorota	Hominin DNA

86

87 Coastal environments and sustained dispersal

88 Population genetics drawn from extant study groups and pioneered in the late 1980s²¹ has

89 revealed an increasingly complex picture of our early global dispersal. The shift in

processing scale and the results emerging from ~~of~~ nuclear and whole genome sequencing in just the last five years (compared to older mtDNA and Y-chromosome studies), and the burgeoning field of ancient DNA (aDNA) analysis, are overturning many previous preconceptions²². Similarity in the modelled depth of genetic lineages among modern Southeast Asian and Australian aboriginal groups compared to those in Africa, together with archaeological evidence for the initial occupation of Australia during the first half of MIS-3 (59-29 ka) encouraged a rapid dispersal model to be advanced²³. This model proposes that the first successful spread of *H. sapiens* followed the southern coasts of the Indian Ocean^{12,24-27} and has been termed the 'Southern Route Dispersal Hypothesis'^{28,29}. Opinion is divided as to the timing and nature of this proposed colonising pulse. Support is still found among some genetic studies for a single successful dispersal, taking place after the supposedly abortive Levantine episode and within a time window 65-55 ka^{13,30}. Others argue either, for an earlier spread into the Middle East³¹ or for multiple dispersals across Eurasia^{25,32,33}, following both southern and potentially northern routes during or before this period. While the rate of genetic advances has been impressive, the rate of archaeological and fossil discoveries has kept pace, though they do not yet mutually reinforce the genetic story in all respects. Indeed they raise significant doubts, if not about a Southern Route model itself, then at least about the simplicity of how it has tended to be presented.

Early Upper Pleistocene sites recently excavated in the Nefud Desert and Empty Quarter of Saudi Arabia (e.g. MDF-61) have been found to contain Levallois technology with affinities comparable to stone tool industries found at sites in the Levant, North Africa and South Asia³⁴⁻³⁶. A long history of episodic occupation within the Arabian interior has been proposed to have likely coincided with pluvial intervals and the expansion of regional rivers and lacustrine systems. The exploitation of inland waterways (as evidenced, for example, at

Jebel Qattar 1, 500 km from the nearest coast) makes a purely coastal dispersal mechanism for early modern human groups (if these were indeed *H. sapiens* as the researchers suspect) less likely than once thought³⁵.

Further to the east, recent survey work on the Kachchh Peninsula, Gujarat (India) – a locale chosen because of its strategic and ecologically favourable position for coastal dispersal – found no substantive evidence for marine exploitation, and a stone tool record from Upper Pleistocene contexts that was in close accordance with the South Asian Middle Palaeolithic. Late Palaeolithic industries that might be attributed to an early MIS-3 dispersal into the subcontinent were absent³⁷. Coastal or not, the possibility of an MIS-5 expansion as far as South Asia – potentially in evidence at sites such as Katoati (95.6±13.1 ka) in the north eastern part of the Thar Desert, and later from the Jwalapuram 3 locality (77±6 ka) in the Jurreru Valley – has been proposed on archaeological and palaeoenvironmental grounds³⁸⁻⁴⁰.

A Southern Route coastal dispersal model also sits somewhat uneasily with the Southeast Asian and Australian records. Leaving aside the taxonomically ambiguous hominin evidence from Callao Cave⁴¹, the earliest directly-dated evidence of less equivocal *H. sapiens* remains – a partial cranium and complete mandible from Tam Pa Ling, Laos (63-46 ka)^{42,43}; together with an upper central incisor and M² from Lida Ajer, Sumatra (68±5 ka)⁴⁴; as well as the new Optically Stimulated Luminescence (OSL) chronology from the non-fossil site of Madjedbebe in Arnhem Land, Australia (c. 65 ka)⁴⁵ – point to an expansion from Africa commencing already at the older end of the range proposed by modern genetic studies, if not earlier. This would have been very close to the age of the Toba super volcanic eruption c. 73 ka⁴⁶, making it a possible driver, though opinion continues to be divided about the effect that Toba is likely to have had on early human populations⁴⁷⁻⁴⁹.

The relationship between coastal proximity and coastal exploitation is also by no means a straightforward one. Palaeolithic sites located on the coast may show little or no evidence of marine exploitation^{37,39}, and even in an insular region like Southeast Asia, there may be a time-lag between access to and incorporation of coastal resources into economic systems⁵⁰. The effect of post-glacial inundation on coastal geography and occupation of Pleistocene coastlines is likely to have been considerable, especially in Southeast Asia^{51,52}. What is apparent, however, is that the earliest sites here, particularly those containing human remains, are often located a considerable distance inland.

While there is currently no formal consensus about what should constitute an effective foraging radius under tropical conditions specifically, ethnographic evidence suggests a coastal zone of exploitation of 5-11 km, with more targeted, logistical expeditions might range up to 30 km from a residential base^{53,54}. None of the earliest fossil-bearing sites in Southeast Asia, thought to reflect *H. sapiens* movement into the region, fall into that range. For example, Tabon Cave on Palawan Island, in the Philippines (*c.* 48 ka), was perhaps the closest: roughly 40 km at -120 m sea level, but remains without evidence of maritime exploitation until the Holocene^{55,56}. Lida Ajer⁴⁴ is *c.* 60 km inland from the modern coast. The Niah Caves, from where the 'Deep Skull' has been directly-dated (by U-Series) to approximately 35 ka, and associated archaeological remains to >46 ka^{57,58}, are situated on the northern Borneo coastal plain, but would have been up to *c.* 80 km from the sea for much of the last glacial period⁵⁹. Tam Pa Ling is approximately 265 km from the nearest modern coast.

This is not to say that there was no contact between the coast and these hinterlands. People or materials were at least periodically moving considerable distances in both directions by the later millennia of the Pleistocene. For example, in Australia, the antiquity of evidence from the Warratyi rock shelter (46-49 ka) implies that dispersal into this

continent probably took a direct north-south route rather than exclusively hugging the coast, and potentially followed or was tied to the resources of river and lake systems in the interior⁶⁰. At the site of Riwi, in north western Australia, fragments of marine *Dentalium* sp. shell, possibly worked into beads, date from 42-29 uncal. ka (uncalibrated ¹⁴C) approximately 300 km from modern coast⁶¹. In northern Vietnam, excavations by the author at Hang Thung Binh 1 have included recovery of a perforated Neritidae (*Neripteron violacea*) shell (Fig. 2). This species favours brackish, transgressive environments, such as those close to river mouths, but was found in a context dating to immediately after the Last Glacial Maximum: c. 17.5 ka, when the coast was as much as 500 km away⁶². Also from northern Vietnam and a similar distance from the modern coast, cowrie shells have been found placed into the eye sockets of an undated but probably mid-Holocene burial excavated at Phia Vai⁶³.

Fig. 2, Excavations at Hang Thung Binh 1, Trảng An, Ninh Binh province, Vietnam. Inset: perforated Neritidae (*Neripteron violacea*) shell, scale: 5 mm (images: R. Rabett & T. Kahlert).

There is also no argument that fully maritime activity would have been required during the Upper Pleistocene to reach Sahul^{64,65} and many parts of island Southeast Asia, such as the North Maluku archipelago (Golo Cave, Gebe Island – 32-29 uncal. ka)⁶⁶, or Sulawesi (Leang Timpuseng – 39.9 ka)⁶⁷. The same could be said for access to the island of Luzon in the Philippines (Callao Cave – 67 ka), though the identity of the hominin responsible for the archaeological record here has not yet been assigned with certainty to *H. sapiens*⁴¹. Pleistocene deposits at the Jerimalai rock shelter on the east coast of East Timor, dated to approximately 42 ka⁶⁸, contain a comparatively abundant and well-preserved faunal assemblage dominated by marine taxa. Among these, turtles and fish – including

fragments from large pelagic species such as tuna – are particularly prominent. The rapid coastal drop-off along this coast will have meant that at no point in its occupational history was the site more than c. 5 km from the sea, making it one of the few locations across the region where initial Pleistocene colonisation might be preserved. The age of the site, however, does not equal the earliest evidence of proposed occupation on East Timor⁶⁹, regionally^{43,58} or in Australia^{45,60,65}. This leaves Jerimalai as a tantalising but not necessarily true reflection of the habits of the earliest colonists to pass through. A fragment of bone hafting technology – possibly from a projectile – recovered at neighbouring Matja Kuru 2 dates to a similar time: 36.5-34.5 ka⁷⁰. This might further attest to the early existence of a projectile technology capable of exploiting marine resources, though here too the link remains unproven and the dates are still comparatively young, relative to any modelled dispersal pulse.

Currently, such evidence as there is for maritime activity along the Southern coastal Route is notable for being heavily weighted towards data coming from Southeast Asia; a region of the world whose geographic history has been defined by periods of inundation and insularity through-out the Pleistocene and Holocene. As such the records as exist may be more representative of adaptive solutions that were particular to this region. Erlandson & Braje have proposed that productive mangrove forests and other estuarine habitats situated along the southern ocean coasts could have provided significant resource opportunities to aid foragers⁷¹, in an extension of their ‘kelp-highway’ model for coastal migration around the North Pacific⁷². While early use of mangrove forests has been discussed and found to be plausible during from the Early Holocene onwards in Southeast Asia⁷³, the underlying issue does not relate so much to specific habitats or their capacity to speed or facilitate dispersal; at issue is a more far-reaching assumption.

One of the features of the Southeast Asian archaeological record is the limited evidence for a pioneer phase of settlement^{56,69,74}. The West Mouth sequence at the Niah Caves (figure 3), one the richest and most extensively studied early *H. sapiens* sites in the region^{57,58,75}, is illustrative of this. From its deepest archaeological contexts there is every indication that those visiting this site belonged to a population that were already comprehensively adapted to the restrictions and affordances of lowland rainforest conditions, be that through the consumption of nuts, such as from *Pangium edule* (Achariaceae) – a tree closely related to Salicaceae (willow/poplar family) – which need to be detoxified before consumption, to the presence of sago and yam starch granules⁷⁶, to the use of plant-based pigments⁷⁷ and effective hunting and probably trapping strategies⁷⁸. There could be various explanations for this. Landscape-learning may have occurred comparatively quickly upon arrival into Southeast Asia, even in the context of hugely diverse tropical environments – such as has been proposed for early human presence in Sri Lanka⁷⁹. Alternatively, knowledge acquired *en-route* could have been cumulative and so only needed to be moderately expanded upon arrival at any new location. Issues of archaeological survey and recovery bias could also still be affecting perceived patterns.

Fig. 3, The West Mouth of the Niah Caves. The principal archaeological investigations took place within the compound (right of picture) (image: G. Barker).

The fact remains that all sites attributed to Pleistocene *H. sapiens* in South Asia and particularly Southeast Asia and Australia are still assumed to have been produced during the same uniparental and genetically successful (i.e. still visible in contemporary human populations) dispersal wave out of Africa. This scenario continues to be speculative, and emerging lines of archaeological and genetic evidence are calling it into question. The notion

that coastal environments between Africa and Sahul might facilitate rapid dispersal has provided a convenient solution to tie together geographically remote yet chronologically similar datasets, particularly genetic datasets. The evidence on the ground, though, does not support such a singular or straightforward explanation.

Inherited complexity

In mainland Asia, there is a growing list of fossil remains from sites in the southern and central provinces of China that purport to contain the remains of *H. sapiens* dating from 125-68 ka⁸⁰⁻⁸². They include the widely publicised recent discovery of 47 teeth (though without any associated archaeology) from the site of Fuyan Cave, Hunan province⁸³. The credibility of these continues to receive a mixed reception^{84,85}, with questions of authenticity being raised on geochronological or taphonomic grounds. Further to south, within the Sundaland extension of Pleistocene mainland Asia, a possible *H. sapiens* P³ (PU-198) has been reported in association with the first appearance of fully modern rainforest taxa (Punung Fauna) on Java⁸⁶, provisionally dated to between 128±15 and 118±3 ka⁸⁷ (contingent upon changes in Java's insularity⁵⁶). This catalogue of osteological evidence raised the possibility of a complex history underpinning early *H. sapiens* populations in eastern Eurasia; something that is also starting to become apparent through the steady publication of extinct human genomes⁸⁸⁻⁹⁰.

The publication in 2010 of mtDNA evidence of an unknown hominin at the Siberian Altai site of Denisova cave⁹¹ has been swiftly followed by considerable widening of the geographic coverage over which 'Denisovan' genetic ancestry can be traced. In addition to substantial (c. 1.2%) ancestral gene flow in New Guinean, Australian and Oceanian groups east of the biogeographic Wallace Line, together with genetic signals for later episodes of

admixture with mainland Southeast Asian modern human groups⁹²⁻⁹⁵, a weaker but widely occurring signal has now been identified in a number of different modern South Asian populations⁹⁶. In 2016 a study hinting that c. 2 % of the modern Papuan genome may have originated from an extinct expansion out of Africa²⁵ has not yet been replicated^{12,97}; however, other complementary data are starting emerge. For example, the Neanderthal genome sequence obtained from remains in Denisova Cave similarly points to introgression of DNA from a *H. sapiens* population that is likely to have diverged from other African groups before the genetic ancestor of all modern non-Africans⁹⁸. These findings further diminish the likelihood that a neatly uniparental dispersal out of Africa was the sole source of early human occupation in eastern provinces of Asia, Southeast Asia or Sahul.

The study of aDNA is providing a critical reassessment of genetic patterns and models constructed from contemporary populations alone and revealing levels of admixture and isolation between ancient and ancestral populations hitherto unseen^{94,95,99,100}. Coverage relating to the period of early human dispersal, however, is still limited and unevenly distributed geographically. Considerable attention has been directed towards fossil remains from higher mid-latitude western and northern Eurasian sites since 2010, when DNA recovered from hominin bones at Vindija Cave (Croatia) and Denisova Cave hailed the first strong evidence for low levels of gene flow from archaic forms to *H. sapiens*^{101,102} (though, in the case of Vindija, new direct dates cast some doubt on this¹⁰³). High coverage genome sequences have lately been recovered from a Denisovan individual¹⁰⁴ and a Neanderthal¹⁰⁵, both from Denisova Cave. Ancient genomes have also been recovered from the remains of early *H. sapiens* at three sites: a juvenile individual (MA-1) from Mal'ta in south-central Siberia (approximately 24 ka)¹⁰⁶; a left femoral fragment from Ust'-Ishim in western Siberia (45-43 ka)¹⁰⁷; and from Kostenki on the Central Russian Plain, where DNA was extracted

from the left tibia of the Kostenki 14 skeleton (38-36 ka)¹⁰⁰. MtDNA and a partial nuclear genome has also been recovered from the lower limb bones of a Pleistocene-aged skeleton at Tianyuan Cave, 50 km southwest of Beijing and dated from 40-37.6 Ka¹⁰⁸.

By comparison, our understanding of human dispersal from lower mid- and low latitude Eurasian sites through aDNA is for the present largely restricted to material from later periods. For example, Douka *et al.* have provided a chronological reassessment and mitochondrial genome from a human temporal bone at Darra-i-Kur, Afghanistan that had been of presumed Pleistocene antiquity¹⁰⁹. Their study produced a much younger age of approximately 4.5 ka, suggesting that the bone was likely intrusive from Neolithic levels at the site. Siska *et al.* have presented genomes for two individuals from Chertovy Vorota (Devil's Gates) in Russia's Primorye Province¹¹⁰. These again date to the Neolithic (approximately 7.7 ka) and exhibit limited affinity to other published ancient genomes. Finding depositional contexts that are conducive to the preservation of aDNA presents a formidable challenge, particularly at tropical latitudes⁸⁸, and one that is compounded by a general paucity of available fossils. A recent study of geoarchaeological considerations in the Southeast Asian tropics lists only 17 Pleistocene-age hominin fossil-bearing sites between the Southern Chinese provinces and Flores (a distance of more than 3500 km)¹¹¹. None of these has as yet yielded viable aDNA, though efforts are on-going.

Although equally at the mercy of the preservation environment, pioneering work to extract hominin aDNA from sediment¹¹² is also set to enhance understanding of ancient populations, their nature and spread. This technique will offer an independent line of evidence to help assess site records, including those associated with dispersal claims, where osteological human remains are absent or sites that are controversial – such as the recent proposal of an MIS-5 butchery site in California^{113,114}. Coupled with the resurgence of

archaeological investigation in eastern Eurasia since the 1990s, and the expanding number of international collaborations in both fields, the potential for new discoveries is substantial. The fundamental rethink of *H. sapiens* dispersal during MIS-5 that has been mooted for some time^{39,55,115-118} may now need to be addressed head-on.

The implications of dispersal success and failure

The genetic record of extant human populations continues to be equivocal about the number and timing of successful dispersals episodes out of Africa, but consistently places such movement in the later first half of the Upper Pleistocene. However, evidence is now accumulating to suggest that whatever happened during that period may well have been significantly underlain by an earlier expansion of our species during MIS-5¹¹⁶. Previously portrayed as 'abortive', new archaeological and genetic research in Arabia, South and Southeast Asia, Australia and China, gives reason to entertain the possibility that the MIS-5 phase of dispersal could have persisted beyond Africa for the best part of 70,000 years (effectively the same time depth we ascribe to the antiquity of today's global population), and could have taken human groups much further afield than previously thought. If this is the case, it begs the question: should evolutionary success be measured only by genetic and demographic continuity into the present?

A wider and more enduring MIS-5 dispersal of *H. sapiens* would have helped to introduce the kind of fragmentary genetic legacy now accepted to have entered our genome from archaic populations. Ultimately that branch of the *H. sapiens* line ended. Establishing the cause of this could turn out to be one of the central questions for Palaeolithic Archaeology and Palaeoanthropology in the coming years. Conceivably, extended isolation, akin to that now proposed for Altai Neanderthal and Denisovan populations⁹⁸ could be

looked to as a factor. While there has been general acceptance that extinction will have been as large-a-driver as innovation has been in our evolutionary history¹¹⁹, the complexities of population interaction and turnover are only now starting to be appreciated fully. Ancient DNA studies are unlocking assumptions about evolutionary affinities and are leading us to reassess archaeological explanations that have been shaped over the last thirty years by a one-sided genomic picture: the history of today's surviving global population.

The effect of early contact on the development and spread of cultural practice may have been no less far-reaching. Under this scenario, we would need to consider in detail the impact that the first 70,000 years of colonization might have had on resident archaic hominin populations and *their* trajectories, rather than attributing causes of change solely to interactions and conditions that arose subsequently. We do not know how events in the former contact period might have affected those in the latter, though the likelihood of early interbreeding between *H. sapiens* and Neanderthals¹⁰⁵ already points to its probable significance. We would need to re-examine the overlap between archaic hominins and anatomically modern humans from second half of the Pleistocene with the possibility that the 'newcomers' may not have been first *H. sapiens* to be met by archaic groups walking into the Eurasian interior or along its coasts. There is also the outside possibility that despite its remote divergence from extant modern human populations¹⁰², a meaningful relationship may exist between the Denisovan signal and an early spread of ancient *H. sapiens*.

Finally, in the context of this paper, some of the earliest archaeological evidence attributed to *H. sapiens* and previously linked to a Southern Route colonization, may prove to be not only better explained by other routes of dispersal, they may also be a record of groups whose descendants did not extend forward through time to the present. The mixed picture of interior and coastal occupation that we have currently from Southeast Asia and

Sahul might be partly explained through a conflation of records. We need to consider the possibility that some current sites in the 45-65 ka range might represent late-surviving enclaves of earlier pioneer *H. sapiens* diaspora, by then in terminal decline, rather than all belonging to the same incoming spread; and that their extinction may even have been hastened by the arrival of people who looked very much like them.

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REFERENCES

1. Vandermeersch, B. The evolution of modern humans: recent evidence from Southwest Asia. Mellars, P. & Stringer, C. (eds.) *The Human Revolution: Behavioural and Biological Perspectives in the Origins of Modern Humans* (Edinburgh University Press, 1989) pp. 155–164.
2. Smith, PJ *A 'Splendid Idiosyncrasy': Prehistory at Cambridge 1915-50*. BAR British Series 485 (Archaeopress, 2009).

3. Grün, R. and Stringer, C. Tabun revisited: revised ESR chronology and new ESR and U-series analyses of dental material from Tabun C1. *Journal of Human Evolution* **39**, 601–612 (2000).
4. Grün, R. *et al.* U-series and ESR analyses of bones and teeth relating to the human burials from Skhul. *Journal of Human Evolution* **49**, 316–334 (2005).
5. McDermott, F., Grün, R., Stringer, C.B., Hawkesworth, C.J. Mass-spectrometric U-series dates for Israeli Neanderthal/early modern hominid sites. *Nature* **363**, 252–255 (1993).
6. Mercier, N. *et al.* The thermoluminescence date for the Mousterian burial of Es-Skhul, Mt. Carmel. *Journal of Archaeological Science* **20**, 169–174 (1993).
7. Stringer, C.B., Grün, R., Schwarcz, H.P., Goldberg, P. ESR dates for the hominid burial site of Es Skhul in Israel. *Nature* **338**, 756–758 (1989).
8. Valladas, H. *et al.* Thermoluminescence dating of Mousterian ‘Proto-Cro-Magnon’ remains from Israel and the origin of modern man. *Nature* **331**, 614–616 (1988).
9. Hershkovitz, I., *et al.* Levantine cranium from Manot Cave (Israel) foreshadows the first European modern humans. *Nature* **520**, 216–219 (2015).
10. Nigst, P. First modern human occupation of Europe: the Middle Danube region as a case study. Boyle, K., Rabett, R., Hunt, C. (eds.) *Living in the Landscape*. (McDonald Institute for Archaeological Research, 2014) pp. 35–48.
11. Endicott, P., Ho, S.Y.W., Metspalu, M., Stringer, C. Evaluating the mitochondrial timescale of human evolution. *Trends in Ecology and Evolution* **24(9)**, 515–521 (2009).
12. Malaspinas, A-S. *et al.* A genomic history of Aboriginal Australia. *Nature*, DOI: 10.1038/nature18299 (2016).

13. Soares, P. *et al.* The Expansion of mtDNA Haplogroup L3 within and Out of Africa. *Molecular Biology and Evolution*. **29(3)**, 915–927 (2012).
14. Mellars, P. Why did modern human populations disperse from Africa *ca.* 60,000 years ago? A new model. *Proceedings of the National Academy of Sciences of the United States of America (PNAS)* **103(25)**, 9381–9386 (2006).
15. Oppenheimer, S. A single southern exit of modern humans from Africa: Before or after Toba? *Quaternary International* **258**, 88–99 (2012).
16. Shea, J.J. Transitions or turnovers? Climatically-forced extinctions of *Homo sapiens* and Neanderthals in the east Mediterranean Levant. *Quaternary Science Reviews* **27**, 2253–2270 (2008).
17. Stewart, J.R. & Stringer, C.B. Human evolution Out of Africa: the role of refugia and climate change. *Science* **335**, 1317–1321 (2012).
18. Hublin, J.-J. *et al.* New fossils from Jebel Irhoud, Morocco and the pan-African origin of *Homo sapiens*. *Nature* **546**, 289–292 (2017).
19. Jacobs, Z. *et al.* The chronostratigraphy of the Haua Fteah cave (Cyrenaica, northeast Libya) d Optical dating of early human occupation during Marine Isotope Stages 4, 5 and 6. *Journal of Human Evolution* **105**, 69–88 (2017).
20. Marean, C.W. *et al.* Early human use of marine resources and pigment in South Africa during the Middle Pleistocene. *Nature* **449**, 905–908 (2015).
21. Cann, R.L., Stoneking, M., Wilson, A.C. Mitochondrial DNA and human evolution. *Nature* **325**, 31–36 (1987).
22. Haber, M., Mezzavilla, M., Xue, Y., Tyler-Smith, C. Ancient DNA and the rewriting of human history: be sparing with Occam’s razor. *Genome Biology* **17** DOI: 10.1186/s13059-015-0866-z (2016).

23. Forster, P. & Matsumura, S. Did early humans go north or south? *Science* **308**, 965–966 (2005).
24. Macaulay, V. *et al.* Single, rapid coastal settlement of Asia revealed by analysis of complete mitochondrial genomes. *Science* **308**, 1034–1036 (2005).
25. Pagani, L. *et al.* Genomic analyses inform on migration events during the peopling of Eurasia. *Nature*. DOI: 10.1038/nature19792 (2016).
26. Rasmussen, M. *et al.* An aboriginal Australian genome reveals separate human dispersals into Asia. *Science*. DOI: 10.1126/science.1211177 (2011).
27. Stoneking, M. & Delfin, F. The human genetic history of East Asia: weaving a complex tapestry. *Current Biology* **20**, R188–R193 (2010).
28. Lahr, M., Foley, R. Multiple dispersals and modern human origins. *Evolutionary Anthropology* **3**, 48–60 (1994).
29. Stringer, C. Coasting out of Africa. *Nature* **405**: 24–27 (2000).
30. Duggan, A.T. & Stoneking, M. Recent developments in the genetic history of East Asia and Oceania. *Current Opinion in Genetics & Development* **29**, 9–14. DOI: 10.1016/j.gde.2014.06.010 (2014).
31. Scally, A. & Durbin, R. Revising the human mutation rate: implications for understanding human evolution. *Nature Reviews: Genetics* **13**, 745–753 (2012).
32. Fregel, R., Cabrera, V., Larruga, J.M., Abu-Amero, K.K., González, A.M. Carriers of mitochondrial DNA Macrohaplogroup N lineages reached Australia around 50,000 years ago following a Northern Asian Route. *PLoS One* **10(6)**, e0129839. DOI: 10.1371/journal.pone.0129839 (2015).
33. Reyes-Centeno, H. *et al.* Genomic and cranial phenotype data support multiple modern human dispersals from Africa and a southern route into Asia. *Proceedings of*

the *National Academy of Sciences of the United States of America (PNAS)* **111(20)**, 7248–7253 (2014).

34. Groucutt, H.S. *et al.* Human occupation of the Arabian Empty Quarter during MIS 5: evidence from Mundafan Al-Buhayrah, Saudi Arabia *Quaternary Science Reviews* **119**, 116–135 (2015).

35. Petraglia, M.D. *et al.* Middle Paleolithic occupation on a Marine Isotope Stage 5 lakeshore in the Nefud Desert, Saudi Arabia. *Quaternary Science Reviews* **30**, 1555–1559 (2011).

36. Scerri, E.M.L. *et al.* Middle to Late Pleistocene human habitation in the western Nefud Desert, Saudi Arabia. *Quaternary International* **382**, 200–214 (2015).

37. Blinkhorn, J., Ajithprasad, P., Mukherjee, A. Did Modern Human Dispersal Take a Coastal Route into India? New Evidence from Palaeolithic Surveys of Kachchh, Gujarat. *Journal of Field Archaeology* DOI: 10.1080/100934690.2017.1323543 (2017).

38. Blinkhorn, J., Achyuthan, H., Petraglia, M., Ditchfield, P. Middle Palaeolithic occupation in the Thar Desert during the Upper Pleistocene: the signature of a modern human exit out of Africa? *Quaternary Science Reviews* **77**, 233–238 (2013).

39. Boivin, N., Fuller, D.Q., Dennell, R., Allaby, R., Petraglia, M.D. Human dispersal across diverse environments of Asia during the Upper Pleistocene. *Quaternary International* **300**, 32–47 (2013).

40. Petraglia, M. *et al.* Middle Paleolithic assemblages from the Indian Subcontinent before and after the Toba super-eruption. *Science* **317**, 114–116 (2007).

41. Mijares, A.S. *et al.* New evidence for a 67,000-year-old human presence at Callao Cave, Luzon, Philippines. *Journal of Human Evolution* **59(1)**, 123–132 (2010).

42. Demeter, F. *et al.* Anatomically modern human in Southeast Asia (Laos) by 46 ka. *Proceedings of the National Academy of Sciences of the United States of America (PNAS)* **109(36)**, 14375–14380 (2012).
43. Demeter, F. *et al.* Early modern Humans and morphological variation in Southeast Asia: fossil evidence from Pa Ling, Laos. *PLoS One* **10(4)**, e0121193. DOI: 10.1371/journal.pone.0121193 (2015).
44. Westaway, K.E. *et al.* An early modern human presence in Sumatra 73,000–63,000 years ago. *Nature* **548**, 322–325 (2017).
45. Clarkson, C. *et al.* Human occupation of northern Australia by 65,000 years ago. *Nature* **547**, 306–310 (2017).
46. Oppenheimer, C. *Eruptions That Shook The World* (Cambridge University Press, 2011).
47. Haslam, M. *et al.* The 74 ka Toba super-eruption and southern Indian hominins: archaeology, lithic technology and environments at Jwalapuram Locality 3. *Journal of Archaeological Science* **37**, 3370–3384 (2010).
48. Williams, M. Did the 73 ka Toba super-eruption have an enduring effect? Insights from genetics, prehistoric archaeology, pollen analysis, stable isotope geochemistry, geomorphology, ice cores, and climate models. *Quaternary International* **269**, 87–93 (2012).
49. Jones, S. Local- and regional-scale impacts of the ~74 ka Toba supervolcanic eruption on hominin populations and habitats in India. *Quaternary International* **258**, 100–118 (2012).
50. Rabett, R. *et al.* Inland shell midden site-formation: investigation into a late Pleistocene to early Holocene midden from Tràng An, northern Vietnam, *Quaternary International* **239**, 153–169 (2011).

51. Hanebuth, T., Stattegger, K., Grootes, P.M. Rapid flooding of the Sunda Shelf: a late-glacial sea-level record. *Science* **288**, 1033–1035 (2000).
52. Soares, P. *et al.* Climate Change and Postglacial Human Dispersals in Southeast Asia. *Molecular Biology Evolution* **25(6)**, 1209–1218 (2008).
53. Erlandson, J.M. The archaeology of aquatic adaptations: paradigms for a new millennium. *Journal of Archaeological Research* **9(4)**, 287–350 (2001).
54. Claassen, C. 1998. *Shells* (Cambridge University Press, 1998).
55. Robles, E.C. Estimates of Quaternary Philippine coastlines, land bridges, submerged river systems and migration routes: A GRASS GIS approach. *Hukay* **18**, 31–53 (2013).
56. Rabett, R.J. *Human Adaptation in the Asian Palaeolithic: Hominin Dispersal and Behaviour during the Late Quaternary* (Cambridge University Press, 2012).
57. Barker, G. (ed.). *Rainforest foraging and farming in island Southeast Asia: the archaeology of the Niah Caves, Sarawak*, Volume 1 (McDonald Institute for Archaeological Research & Sarawak Museums, 2013).
58. Barker, G. & Farr, L. (eds.). *Archaeological investigations in the Niah Caves, Sarawak*, Volume 2 (McDonald Institute for Archaeological Research & Sarawak Museums, 2016).
59. Hunt, C.O. & Gilbertson, D.D. Shorelines, mangroves and human environments in the coastal lowlands of northeastern Borneo during the Late Quaternary. Boyle, K., Rabett, R., Hunt, C. (eds.) *Living in the Landscape* (McDonald Institute for Archaeological Research, 2014) pp. 121-136.
60. Hamm, G. *et al.* Cultural innovation and megafauna interaction in the early settlement of arid Australia. *Nature* DOI: 10.1038/nature20125 (2016).
61. Habgood, P.J. & Franklin, N.R. The revolution that didn't arrive: A review of Pleistocene Sahul. *Journal of Human Evolution* **55**, 187–222 (2008).

62. Yao, Y-T., Harff, J., Meyer, M., Zhan, W-H. Reconstruction of paleocoastlines for the northwestern South China Sea since the Last Glacial Maximum. *Science in China Series D: Earth Sciences* **52(8)**, 1127–1136 (2009).
63. Cuong, N.L. Unique burial practice by ancient cavemen of the Hoa Binh civilisation in Vietnam. *Anthropologischer Anzeiger* **65(2)**, 129–135 (2007).
64. O'Connell, J.F. & Allen, J. The process, biotic impact, and global implications of the human colonization of Sahul about 47,000 years ago. *Journal of Archaeological Science* **56**, 73–84 (2015).
65. Veth, P. et al. Early human occupation of a maritime desert, Barrow Island, North-West Australia. *Quaternary Science Reviews* **168**, 19–29 (2017).
66. Szabó K., Brumm, A., Bellwood, P. Shell Artefact Production at 32,000–28,000 BP in Island Southeast Asia Thinking across Media? *Current Anthropology* **48(5)**, 701–723 (2007).
67. Aubert, M. et al. Pleistocene cave art from Sulawesi, Indonesia. *Nature* **514**, 223–227 (2014).
68. O'Connor, S. New evidence from East Timor contributes to our understanding of earliest modern human colonisation east of the Sunda Shelf. *Antiquity* **81**, 523–535 (2007).
69. Hawkins, S. et al. Oldest human occupation of Wallacea at Laili Cave, Timor-Leste, shows broad-spectrum foraging responses to late Pleistocene environments. *Quaternary Science Reviews* **171**, 58–72 (2017).
70. O'Connor, S., Robertson, G., Aplin, K.P. Are osseous artefacts a window to perishable material culture? Implications of an unusually complex bone tool from the Late Pleistocene of East Timor. *Journal of Human Evolution* **67**, 108–119 (2014).

71. Erlandson, J.M. & Braje, T.J. Coasting out of Africa: The potential of mangrove forests and marine habitats to facilitate human coastal expansion via the Southern Dispersal Route. *Quaternary International* **382**, 31–41 (2015).
72. Erlandson, J.M. & Braje, T.J. From Asia to the Americas by boat? Paleogeography, paleoecology, and stemmed points of the northwest Pacific. *Quaternary International* **239**, 28–37 (2011).
73. Rabett, R.J. The early exploitation of Southeast Asian mangroves: bone technology from caves and open sites. *Asian Perspectives* **44(1)**, 154–79 (2005).
74. Anderson, A. & O'Connor, S. Indo-Pacific migration and colonization – Introduction. *Asian Perspectives* **47(1)**, 2–11 (2008).
75. Barker, G. *et al.* The ‘human revolution’ in tropical Southeast Asia: the antiquity and behaviour of anatomically modern humans at Niah Cave (Sarawak, Borneo). *Journal of Human Evolution* **52**, 243–261 (2007).
76. Barton, H. The case for rainforest foragers: the starch record at Niah Cave, Sarawak. *Asian Perspectives* **44(1)**, 56–72 (2005).
77. Pyatt, F.B., Barker, G.W., Rabett, R.J., Szabó, K., Wilson, B. Analytical examination of animal remains from Borneo: The painting of bone and shell. *Journal of Archaeological Science* **37(9)**, 2102–2105 (2010).
78. Piper, P. & Rabett, R. Vertebrate fauna from the Niah Caves. Barker, G. & Farr, L. (eds.) *Archaeological investigations in the Niah Caves, Sarawak*, Volume 2 (McDonald Institute for Archaeological Research, 2016) pp. 401–437.
79. Roberts, P. *et al.* Fruits of the forest: Human stable isotope ecology and rainforest adaptations in Late Pleistocene and Holocene (~36 to 3 ka) Sri Lanka. *Journal of Human Evolution* **106**, 102–118 (2017).

80. Li, Z-Y. *et al.* Late Pleistocene archaic human crania from Xuchang, China. *Science* **355**, 969–972 (2017).
81. Liu, W. *et al.* Human remains from Zhirendong, South China, and modern human emergence in East Asia. *Proceedings of the National Academy of Sciences of the United States of America (PNAS)* DOI: 10.1073/pnas.1014386107 (2010).
82. Shen, G. *et al.* U-Series dating of Liujiang hominid site in Guangxi, Southern China. *Journal of Human Evolution* **43**, 817–829 (2002).
83. Liu, W. *et al.* The earliest unequivocally modern humans in southern China. *Nature* DOI: 10.1038/nature15696 (2015).
84. Dennell, R. *Homo sapiens* in China 80,000 years ago. *Nature* **526**, 647–648 (2015).
85. Michel, V. *et al.* The earliest modern *Homo sapiens* in China? *Journal of Human Evolution* **101**, 101–104 (2016).
86. Storm, P. *et al.* Late Pleistocene *Homo sapiens* in a tropical rainforest fauna in East Java. *Journal of Human Evolution* **49**, 536–545 (2005).
87. Westaway, K. *et al.* Age and biostratigraphic significance of the Punung Rainforest Fauna, East Java, Indonesia, and implications for *Pongo* and *Homo*. *Journal of Human Evolution* **53(6)**, 709–717 (2007).
88. Nielsen, R. *et al.* Tracing the peopling of the world through genomics. *Nature* **541**, 302–310 (2017).
89. Pääbo, S. The diverse origins of the human gene pool. *Nature Reviews – Genetics* **16**, 313–314 (2015).
90. Vernot, B. & Akey, J.M. Complex history of admixture between Modern Humans and Neandertals. *The American Journal of Human Genetics* **96**, 448–453 (2015).
91. Krause, J. *et al.* The complete mitochondrial DNA genome of an unknown hominin from southern Siberia. *Nature* **464**, 894–897 (2010).

92. Cooper, A. & Stringer, C.B. Did the Denisovans cross Wallace's Line? *Science* **342**, 321–323 (2013).
93. Qin, P. & Stoneking, M.. Denisovan ancestry in East Eurasian and Native American populations. *Molecular Biology and Evolution* **32(10)**, 2665–2674 (2016).
94. Reich, D. *et al.* Denisova admixture and the first modern human dispersals into Southeast Asia and Oceania. *The American Journal of Human Genetics* **89**, 516–528 (2011).
95. Skoglund, P. & Jakobsson, M. Archaic human ancestry in East Asia. *Proceedings of the National Academy of Sciences of the United States of America (PNAS)* **108(45)**, 18301–18306 (2011).
96. Sankararaman, S., Mallick, S., Patterson, N., Reich, D. The combined landscape of Denisovan and Neanderthal ancestry in present-day humans. *Current Biology* **26**, 1– 7 (2016).
97. Mallick, S. *et al.* The Simons Genome Diversity Project: 300 genomes from 142 diverse populations *Nature* **538**, 201–206 (2016).
98. Kuhlwilm, M. *et al.* Ancient gene flow from early modern humans into Eastern Neanderthals. *Nature* DOI: 10.1038/nature16544 (2016).
99. Fu, Q. *et al.* An early modern human from Romania with a recent Neanderthal ancestor. *Nature* DOI: 10.1038/nature14558 (2015).
100. Seguin-Orlando, A. *et al.* Genomic structure in Europeans dating back at least 36,200 years. *Science* DOI: 10.1126/science.aaa0114 (2014).
101. Green, R.E. *et al.* A Draft Sequence of the Neandertal Genome. *Science* **328**, 710–722 (2010).

102. Reich, D. *et al.* Genetic history of an archaic hominin group from Denisova Cave in Siberia. *Nature* **468**, 1053–1060 (2010).
103. Devière, T. *et al.* Direct dating of Neanderthal remains from the site of Vindija Cave and implications for the Middle to Upper Paleolithic transition. *Proceedings of the National Academy of Sciences of the United States of America (PNAS)* **114**(40), 10606–10611.
104. Meyer, M. *et al.* A High-Coverage Genome Sequence from an Archaic Denisovan Individual. *Science Express* DOI: 10.1126/science.1224344 (2012).
105. Prüfer, K. *et al.* The complete genome sequence of a Neanderthal from the Altai Mountains. *Nature* **505**, 43–49 (2014).
106. Raghavan, M. *et al.* Upper Palaeolithic Siberian genome reveals dual ancestry of Native Americans. *Nature* DOI:10.1038/nature12736 (2013).
107. Fu, Q. *et al.* Genome sequence of a 45,000-year-old modern human from western Siberia. *Nature* **514**, 445–449 (2014).
108. Fu, Q. *et al.* DNA analysis of an early modern human from Tianyuan Cave, China. *Proceedings of the National Academy of Sciences of the United States of America (PNAS)* DOI: 10.1073/pnas.1221359110 (2013).
109. Douka, K. *et al.* Direct radiocarbon dating and DNA analysis of the Darra-i-Kur (Afghanistan) human temporal bone. *Journal of Human Evolution* **107**, 86–93 (2017).
110. Siska, V. *et al.* Genome-wide data from two early Neolithic East Asian individuals dating to 7700 years ago. *Science Advances* **3**, e1601877 (2017).

111. Morley, M. The geoarchaeology of hominin dispersals to and from tropical Southeast Asia: A review and prognosis. *Journal of Archaeological Science* **77**, 78–93 (2017).
112. Slon, V. *et al.* Neandertal and Denisovan DNA from Pleistocene sediments *Science* DOI: 10.1126/science.aam9695 (2017).
113. Holen, S.R. *et al.* A 130,000-year-old archaeological site in southern California, USA. *Nature* **544**: 479–483 (2017).
114. Braje, T.J. *et al.* Were Hominins in California ~130,000 Years Ago? *PaleoAmerica* **3(3)** DOI: 10.1080/20555563.2017.1348091 (2017)
115. Dennell, R. & Petraglia, M. The dispersal of *Homo sapiens* across southern Asia: how early, how often, how complex? *Quaternary Science Reviews* **47**, 15–22 (2012).
116. Groucutt, H.S. *et al.* Rethinking the dispersal of *Homo sapiens* out of Africa. *Evolutionary Anthropology* **24**, 149–164 (2015).
117. Petraglia, M.D., Haslam, M., Fuller, D.Q., Boivin, N., Clarkson, C. Out of Africa: new hypotheses and evidence for the dispersal of *Homo sapiens* along the Indian Ocean rim. *Annals of Human Biology* **37(3)**, 288–311 (2010).
118. Rabett, R.J. Techno-modes, techno-facies and palaeo-cultures: change and continuity in the Pleistocene of Southeast, Central and North Asia. Roberts, B. & Vander Linden, M. (eds.) *Investigating Archaeological Cultures: Material Culture, Variability and Transmission* (Springer Publishing, 2011) pp. 97–136.
119. Lahr, M.M. & Foley, R.A. Towards a theory of modern human origins: geography, demography, and diversity in recent human evolution. *Yearbook of Physical Anthropology* **41**, 137–176 (1998).